# Observation of Mammalian Similarity through Allometric Scaling Laws

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ABSTRACT

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We discuss the problem of observation of natural similarity in skeletal evolution of terrestrial mammals. Analysis is given by means of testing of the power scaling laws established in long bone allometry, which describe development of bones (of length $L$ and diameter $D$) with body mass in terms of the growth exponents, *e.g.* $\lambda = d\log L/d\log D$ . The bone-size evolution scenario given three decades ago by McMahon was quiet explicit on the geometrical-shape and mechanical-force constraints that predicted $\lambda = 2/3$. This remains too far from the mammalian allometric exponent $\lambda^{(\exp)} = 0.80 \pm 0.2$, recently revised by Christiansen, that is a chief puzzle in long bone allometry. We give therefore new insights into McMagon's constraints and report on the first observation of the critical-elastic-force, bending-deformation, muscle-induced mechanism found with $\lambda = 0.80 \pm 0.3$. This mechanism governs the bone-size evolution with avoiding skeletal fracture caused by muscle-induced peak stresses and is expected to be a unique for small and large mammals.

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*Keywords:* allometric scaling , long bones, muscles, mammals.

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**PACs numbers:** 87.10.+e, 87.19.Ff, 87.23.Kg.

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## I. INTRODUCTION

In general, biological laws do not follow from physical laws in a simple and direct way. Examples include Kleiber's allometric law known as the 3/4 power law that scales metabolic rates for animals and plants to their mass. As shown by West *et al.* in Refs. [1,2] the observed metabolic rate scaling law arises from the interplay between geometric and physical constraints implicit in the energy source distributions (see also discussion in Ref. [3]). Another famous 2/3 power law for scaling of longitudinal-to-transverse dimensions of animals and plants was proposed by McMahon [4] through physical description of geometric-shape and critical-force similarities noticed in size evolution of animals and plants. Given in explicit form in Ref. [4], the geometrical-(cylindrical-volume)-shape and mechanical-(critical-elastic-buckling)-force constraints imposed on size evolution for animals and plants with their mass yielded the aforementioned 2/3 power scaling law, along with the 1/4 and 3/8 laws deduced [4], respectively, for longitudinal and transverse linear dimensions. During almost three decades McMahon's scaling laws have been a controversial subject of intensive study and debate. As the matter of fact, McMahon's description of the geometrical-shape and mechanical-force similarities was experimentally proved for terrestrial mammals neither in body allometry [5] nor in long bone allometry [6,8–15]. Moreover, the most recent condemnation by Christiansen [14] states that no satisfactory explanation for any power-law scaling observed in mammalian allometry can be expected.

We will demonstrate that the essence of the problem of failure of McMahon's constraints is due to the fact that the skeletal subsystem of animals is not mechanically isolated from their muscle subsystem, as was suggested in Ref. [4]. Also, McMahon's hypothesis that the skeletal support of weight and fast locomotion of mammals is driven solely by a gravitation field contradicts to up-to-date comprehension on a role of muscle fibers and tendons in formation of maximum skeletal stresses. The paper is organized as follows. In Sec.II, we revisit McMahon's evolution constraint equations within context of their application to long bone allometry for terrestrial mammals. In view of the known experimental findings in muscle fiber allometry, these equations are modified and generalized . Experimental testing of the two distinct critical-elastic-force mechanisms that govern evolution of mammalian bones is elaborated in Sec. III. Discussion and conclusions are given in Sec. IV.

## II. MCMAGON'S CONSTRAINTS IN LONG BONE ALLOMETRY

### A. Elastic Similarity Model Revisited

Famous power laws by McMahon [4] for scaling of linear dimensions of animals and plants was proposed within the framework of the so-called elastic similarity model (hereafter, ESM). Application of the ESM by McMahon to the case of mammalian bone allometry was based on the *cylindric-shape* correspondence that takes place between a given skeletal bone and a cylindrical beam. A bone sample was therefore geometrically approximated by a cylinder of diameter $D_{is}$ and length $L_{is}$, where index $i$ counts different bones and $s$ indicates mammalian specie. The *mechanical-force* correspondence to the same *rigid* cylinder is justified by observation of the universal (specie-independent) bone-stress safety factors. These are given by ratio of yield stress to peak stress and are about 3. Exploration of such a kind of the mechanical correspondence by McMahon gave rise to the maximum-(elastic-buckling)-force *constraint* imposed on volume-size evolution of a given bone.

More specifically, the ESM is based on the fact that the mechanical failure of a bone is prevented through its linear dimensions $D_{is}$ and $L_{is}$, adjusted to bear critical *buckling deformations*, related to peak stresses through the maximum elastic forces: $F^{(\max)}_{elast} = F^{(crit)}_{buckl}$. The latter is due the elastic instability given in terms of the critical bending deformations and is described by the Euler critical estimate $F^{(crit)}_{buckl} = \pi^2 EI/L^2$ for a given cylinder (of length

$L$ and of diameter $D$, with the moment of inertia $I = \pi D^4/64$ and the elastic modulus $E$, see *e.g.* Cap. IV in Ref. [16]). Thus the ESM constraint equations attributed by McMahon to the cylindric-shape and elastic-force similar skeletal bones, can be introduced through $(a)$ the elastic-buckling critical force $F_{is}^{(crit)}$ and $(b)$ the cylindric-bone volume $V_{is}^{(bone)}$, namely

$$F_{is}^{(crit)} = \frac{\pi}{64} E \frac{D_{is}^4}{L_{is}^2} \tag{1a}$$

$$V_{is} = D_{is}^2 L_{is} \ . \tag{1b}$$

In long-bone allometry, the observation of evolution of limb bones across mammalian species is discussed though the bone-size, linear-dimension scaling to body mass $M_s$. This is given in terms of the bone-diameter and the bone-length allometric exponents $d_i$ and $l_i$, or of the $i$-bone *growth dimension exponents*, introduced by the following scaling differential relations, namely

$$d_i = \frac{d \log D_{is}}{d \log M_s}, \ l_i = \frac{d \log L_{is}}{d \log M_s}, \ \text{and} \tag{2}$$

$$\lambda_i = \frac{d \log L_{is}}{d \log D_{is}} \equiv \frac{l_i}{d_i}. \tag{3}$$

The *reduced dimension* exponent $\lambda_i$, related to the longitudinal-to-transverse scaling, is also defined. As seen, Eqs.(2), (3) are equivalent to the corresponding differential equations $dD_{is}/dM_s = d_i D_{is}/M_s$ , etc., which solutions are commonly derived in bone allometry through regression equations $D_{is} = c_{is} M^{d_i}$, where $M$ is treated as an external mammalian parameter and $c_{is}$ are constants. A notable feature of the introduced scaling relations is independence of the $i$-bone exponents on mammalian specie $s$. This is corroborated in bone allometry observations and Eqs. (2), (3) are therefore commonly treated as the allometric *scaling laws*. This implies a universal fashion in evolution of any linear dimension of bones, as well as bone *volume* $V_{is} = D_{is}^2 L_{is}$, with body mass that in a certain way reflects similarity of mammals with their size evolution. With taking into account that $\rho V_{is} = M_{is}$ ($\rho$ is bone density), and adopting additionally McMahon's hypotheses $(a)$ that an effective skeletal evolution is constrained by gravitation, i.e., $F_{is}^{(crit)} \sim g M_{is}$ ($g$ is the gravity constant), and

($b$) that bone mass $M_{is}$ linearly scales to body mass $M_s$, the following $i$-bone-evolution equations, namely

$$\begin{cases} 4d_i - 2l_i = 1, \\ 2d_i + l_i = 1 \end{cases} \tag{4}$$

result from, respectively, Eqs.(1a) and (1b) with the help of the scaling relations given in Eq.(2). In turn, Eqs.(4) and (3) provide the well known ESM predictions: $d_0^{(buckl)} = 3/8$, $l_0^{(buckl)} = 1/4$, and $\lambda_0^{(buckl)} = 2/3$, including the trivial *isometric* solution $d_0 = l_0 = 1/3$ and $\lambda_0 = 1$. As mentioned in the Introduction, these predictions were not proved experimentally even when a statistical dispersion of allometric data was taken into account (for recent criticism of the ESM predictions for the exponents $d$, $l$ and $\lambda$ see analyses given in Table 5 in Refs. [13] and Table 3 in Ref. [14], respectively).

### B. Elastic-Buckling-Force Criterium

Skeletal evolution of animals cannot be studied independently of their muscle fibers and tendons. Moreover, the peak skeletal stresses are generated rather by muscle contractions than by gravitation. These both statements follow from studies of muscle design and bone strains during locomotion [17,18,20,21]. We infer therefore that the maximum elastic forces exerted by long bones are originated from the *maximum* muscle forces, *i.e.*, $F_{elast}^{(\max)} = F_{musc}^{(\max)}$. The same studies provide strong evidence that the maximum muscle stresses are independent of body mass, and thus $F_{musc}^{(\max)}/A_{musc}^{(\max)} \propto M^0$, where $A_{musc}^{(\max)}$ is the maximum cross-section area of muscle fibers. The critical-force constraint, justified through the safety factors, can be therefore formally introduced into consideration by the "overall-bone" critical-force exponent $a_c$, namely

$$a_c = \frac{d \log F_{musc}^{(crit)}}{d \log M_s} = a_{cm} = \frac{d \log A_{musc}^{(\max)}}{d \log M} \tag{5}$$

and the *critical muscle-area* exponent $a_{cm}$. These should be distinguished from the corresponding exponents

$$a_{ci} = \frac{d \log F_{is}^{(crit)}}{d \log M_s} \text{ and } a_m = \frac{d \log A_{musc}}{d \log M} \tag{6}$$

where $F_{is}^{(crit)}$ is given in Eq.(1a). The muscle-area exponent $a_m$ is known in muscle allometry [9,20,22,19] as the muscle-fiber, cross-section-area exponent and can be exemplified by data $a_m^{(\exp)} = 0.69 - 0.91$ derived by Pollock and Shadwick for four distinct groups of muscles in mammalian hindlimbs (see Fig.3 in Ref. [22]). Commonly, the maximum muscle force is associated [9] with the leg group of muscles of animals, *i.e.*, $A_{musc}^{(\max)} = A_{musc}^{(leg)}$. With adopting of the latter in Eq.(5), the "leg-muscle" critical exponent $a_{cm}^{(\exp)} = 0.81 - 0.83$ was obtained [22] (on the bases of data [9] for six groups of mammalian leg muscles by Alexander *et al.*) and reported by Pollock and Shadwick in Ref. [22].

In order to establish the critical muscle-area exponent $a_{cm}^{(\exp)}$ introduced in Eq.(5), we have reanalyzed the experimental data found in Ref. [22] on muscle fiber area $A_{musc}$ in mammalian hindlimbs as a function of body mass. In **Fig.1** we seek therefore the maximum areas $A_{musc}^{(\max)}$ that are provided by the highest points $A_{musc}$ found for a given mass. As seen from Fig.1, $A_{musc}^{(\max)}$ are due to different groups of leg muscles, which change with evolution of (35 quadrupedal) animals from small to large species. No doubts that the muscle group *common digital extensors* (shown by crosses and adjusted [22] with $a_m^{(C)} = 0.69$) has the smallest areas, shows almost isotropic evolution, and does not therefore plays any important role in formation of maximum muscle stresses. Qualitatively the same can be referred to *plantaris* (shown by circles) with [22] $a_m^{(P)} = 0.91$. If one excludes these groups, a rough estimate for the critical muscle-area exponent $a_{cm}$ can be given by $a_{cm}^{(\exp)} \approx 0.77 - 0.85$. This follows from the analysis given in Ref. [22] and adjusted for the *principal* muscles (defined here through the groups of *gastsrocnemius* with $a_m^{(G)} = 0.77$ and *deep digital flexors* with $a_m^{(D)} = 0.85$ ), which are eventually responsible for maximum hindlimbs bone stresses. More accurate data on maximum area $A_{musc}^{(\max)}$ is found by fitting the experimental points asymptotically from above that is shown by the solid line in Fig.1. Regression elaborated within the experimental error (approximated from above by a set of nearest points measured for the same mass) provides $a_{cm}^{(\exp)} = 0.82 \pm 0.01$ (with the correlation coefficient $r = 0.997$).

Remarkably, that this finding matches well the aforegiven data for the "leg-muscle" exponent by Alexander *et al.* reported in Ref. [22] and can be therefore considered as the reliable data.

Eqs.(5) and (6) yield the following definition for the "overall-bone" averaged exponents, namely

$$a_c =< a_{ci} >\equiv \frac{1}{n}\sum_{i=1}^{n} a_{ci} = a_{cm}, \tag{7}$$

where summation is limited by bones which do play a *principal* role in support and fast locomotion of body mass of animals. Eq.(7) can be also treated as an extension of the similar definition of the *mammalian* principal-bone-averaged exponents $d$, $l$ and $\lambda$ introduced with the help of Eqs.(2),(3), *e.g.*, $d =< d_i >$. Thereby, the modification of McMahon's $a$-hypothesis provides a new $a$-constraint equation imposed on the exponents: $4d - 2l = a_c$.

In view of the fact that neither skeletal mass [11] nor bone mass [15] are linear with mammalian body mass, McMahon's revised $b$-constraint equation given in Eq.(4) for $i$-bone should be substituted by $2d_i + l_i = b_i$, where the *i-bone-mass* exponent $b_i$ is introduced through the relevant scaling, namely

$$b_i = \frac{d \log M_{is}}{d \log M_s}. \tag{8}$$

Thus, McMahon's critical-force and cylindric-shape constraints given in Eq.(4) result in the following modifications of the ESM, namely

$$\begin{cases} 4d - 2l = a_c, \\ 2d + l = b \end{cases} . \tag{9}$$

In turn, this provides new predictions for the mammalian overall-bone dimension and reduced-dimension exponents, or the *elastic-buckling-criterium* predictions, namely

$$d^{(buckl)} = \frac{a_c + 2b}{8}\ , \ l^{(buckl)} = \frac{2b - a_c}{4} \ \text{and} \tag{10}$$

$$\lambda^{(buckl)} = 8 < \frac{b_i}{a_{ci} + 2b_i} > -2\ . \tag{11}$$

The latter prediction follows from the definition for the reduced-dimension exponent $\lambda_i = l_i/d_i$ given in Eq.(3) and presented here in the form $\lambda_i = b_i/d_i - 2$, with the help of the $b$-constraint equation.

### C. Elastic-Bending-Force Criterium

After Alexander *et al.* [23] it has been widely recognized (for recent references see in Ref. [15]) that the elastic *bending* deformations play a crucial role in the overall peak stresses of long bones instead of a simple axial compression discussed [4] in terms of buckling deformations by McMahon. The corresponding critical force $F_{elas}^{(\max)} = F_{bend}^{(crit)}$ applied normally to the bone before fracture was discussed in long-bone allometry in Refs. [11,20]. In view of the common elastic nature of both kind of deformations, the force $F_{bend}^{(crit)}$ in a certain way extends the ESM given in Eq.(1) to the case of the bending critical deformations, namely

$$F_{is}^{(crit)} \sim E\frac{D_{is}^3}{L_{is}} \tag{12a}$$

$$\rho D_{is}^2 L_{is} = M_{is} \tag{12b}$$

Straightforward application of the scaling differential relations given in Eqs. (2),(3), with accounting of the critical-force and the bone-mass growth exponents given in, respectively, Eqs.(5), (8) and (9), results in the following new constraint equations, namely

$$\begin{cases} 3d - l = a_c, \\ 2d + l = b. \end{cases} \tag{13}$$

This provides the *elastic-bending criterium* expressed in terms of the following predictions for the mammalian bone-dimension growth exponents, namely

$$d^{(bend)} = \frac{a_c + b}{5}\ ,\ l^{(bend)} = \frac{3b - 2a_c}{5} \text{ and} \tag{14}$$

$$\lambda^{(bend)} = 5 < \frac{b_i}{a_{ci} + b_i} > -2 \tag{15}$$

Notably that both the elastic-force criteria given in Eqs. (10) and (14) are consistent with the isometric solution ($d_0 = l_0 = 1/3$ and $\lambda_0 = 1$), which exists under conditions that the mammalian muscle-area subsystem develops isometrically ($a_0 = 2/3$) and independently of the skeletal subsystem ($b_0 = 1$). As a matter of fact, this simplified geometric scenario is violated by the nature through the bone-dimension allometric scaling laws given by $d^{(\exp)} > 0.33$, $l^{(\exp)} < 0.33$, and $\lambda^{(\exp)} < 1$.

## III. OBSERVATION OF BONE EVOLUTION SIMILARITIES THROUGH EXPERIMENTAL TESTING OF CONSTRAINT EQUATIONS

All predictions given by the original [4], modified and extended ESM are analyzed in the bone growth diagram in **Fig.2**. As seen, the available experimental data matches neither the isometric nor the original ESM solutions (shown by crosses), even in case when dispersion effects of the experimental data (shown by error bars) are taken into account. Note that this large dispersion is not caused by error measurements of bone dimensions or body mass of animals, but is result from a large phylogenetic spectrum of terrestrial mammals*. Unlike the case of the pioneer data [8] by Alexander *et al.*, all species which have multiple specimens, were additionally averaged [14] within a certain mammalian subfamily before to be documented. The most accurate allometric data with the systematically reduced phylogenetic statistical error were given [13–15] by Christiansen.

The predictions of the modified and the extended ESM are shown in Fig. 2 by the shaded areas, which correspond to, respectively, Eqs.(9) and (13) estimated with account of the reliable domain for the critical-force exponent $a_c^{(\exp)} = 0.81 - 0.83$ and of that for the bone-mass exponent $b^{(\exp)} = 1.0 - 1.1$, which approximately covers dispersion of the experimental data on $b_i^{(\exp)}$( see Table 2 in Ref. [15]). The shaded areas correspond the critical-force constraints given by the $a$-constraint lines $4d - 2l = 0.82$ and $3d - l = 0.82$ extended by cylindric-volume constraints implicit in the form of the elastic-buckling-force and the elastic-bending-force criteria, respectively. As seen from Fig. 2, the elastic-*buckling* criterium seems to be observable within the range of the unreduced phylogenetic statistical error. After reduction of this error, only the elastic-*bending* criterium corroborates.

Besides the case of the 6-long-bone-averaged allometric data [13] given in Fig.2 for the

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*In fact, there exist some errors due to deviation of bone shape from the ideal cylinder. Also, not all body mass were really measured but taken as an average from the literature data (see discussion in Ref. [14]).

*one-scale* least-square regression (*LSR*), we have also elaborated analysis of the double set of the allometric exponents (taken from Table 5 in Ref. [13]) derived within the *two-scale* regressions made for small ($M < 50kg$) and large ($M > 50kg$) mammals. But no definitive conclusions on domination of any elastic-force criteria is inferred. Indeed, in the case of the overall-(6-bone)-averaged data fro small and large animals is far to be fitted by the dashed areas in Fig.2. When the *ulna* and the *fibula* are excluded, the principal-(4-bone)-averaged *LSR* data corroborates the elastic-bending criterium and the elastic-buckling criterium, respectively, for small and large mammals. However, unlike the case of the one-scale data, experimental accuracy of the two-scale analysis is marginal that makes doubtful the inference on observation of both the distinct critical-force constraints. In what follows we restrict our analysis by the one-scale allometric data for the four principal mammalian long bones listed in **Table 1**.

First, we check a *selfconsistency* of data on the dimension ( $l_i^{(\mathrm{exp})}$, $d_i^{(\mathrm{exp})}$ ) [13] and reduced-dimension ($\lambda_i^{(\mathrm{exp})}$ ) [14] allometric exponents obtained independently and presented in first and second columns of Table 1, respectively. As seen, the bone-averaged data, when are compared between the two regression methods, obey the relation $d^{(\mathrm{exp})}/l^{(\mathrm{exp})} = \lambda^{(\mathrm{exp})}$ with accuracy that is much higher for case partial $i$-bone relations $d_i^{(\mathrm{exp})}/l_i^{(\mathrm{exp})} = \lambda_i^{(\mathrm{exp})}$ compared within the scope of the same method. Then, the geometrical mammalian similarity is tested on the basis of the $b$-constraint equation $2d_i^{(\mathrm{exp})} + l_i^{(\mathrm{exp})} = b_i^{(\mathrm{exp})}$ in second and third columns of Table 1. Again, the cylindric-shape similarity, given in terms of the bone-averaged data, is confirmed† with a small error. We deduce that the observation of the mammalian similarity through the allometric power laws can be realized only "on the average", but not for a given type of "mammalian" bone as it commonly adopted in allometric studies. Examples are testing of the original ESM predictions (and the constraint equation $3d - l = a$) in Table 5

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†Exclusion should be given for the case of the exponent $b^*$ , which data obtained by the square regression (LSR) method is not available.

in Ref. [13], Table 3 in Ref. [14] (and Table 3.11 in Ref. [19]) that is made for data a given $i$-bone, but not for the overall-bone data.

The validation of the bone-evolution $a$-constraint equation for the case of the bending loads, *i.e.*, $3d-l=a$, where $a$ is treated as a free parameter, was first discussed [20] by Selker and Carter in terms of the bone strength index. On the basis of the mammalian data [10] by Biewener (shown in Fig. 2) and their own data for *artiodactyls*, the overall-bone-averaged equation $3d^{(\mathrm{exp})}-l^{(\mathrm{exp})}=a$ provided [20] estimates $a=0.77$ and $0.82$, respectively. In view of the closeness of these bone-dimension allometric prediction to the known [20] muscle-area allometric exponent $a_m^{(\mathrm{exp})}=0.77-0.82$ it was claimed [20] that the bending or torsion deformations in mammalian long bones are due to muscle contractions. The same analysis given on the basis of other available in the biological literature allometric data, including the particular case of birds[‡], has been recently made [19] by Garcia. As the result, a prediction for the allometric muscle-area exponent $a_m=0.80$ (which corresponds to the mean value of the aforementioned mammalian data $a_m^{(\mathrm{exp})}$ and that for birds) was suggested [19] as the credible data for experimental testing of the bending-force-constraint equation.

As follows from the pioneer work [4] by McMahon, and elucidated in the previous section, the force-constraint equation is driven by *critical* force, and is therefore given as $3d-l=a_c$ where the critical-force exponent, according to Eq.(7), is established by the data on maximum-muscle-area allometry, i.e., $a_c=a_{cm}^{(\mathrm{exp})}=0.82\pm0.01$. We have therefore reconsidered analysis given in Table 3.11 in Ref. [19] and found [24] that no conclusions can be made on validation[§] on the principal-bone averaged equation $3d^{(\mathrm{exp})}-l^{(\mathrm{exp})}=a_{cm}^{(\mathrm{exp})}$ on the bases of the two-scale, *RMA* and *LSR* data [13]. Conversely, the *critical*-bending-force constraint equation $3d-l=a_c$ is strongly supported by the *one-scale* data [13] by Christiansen deduced through both the different (LSR and RMA) regressions. This follows

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[‡]Application of the ESM for birds remains questionable.

[§]Again, the marginal estimate $a_{cm}=0.829$ has obtained in the case of the small-animal *LSR* data.

from the bone-dimension predictions $a_c = 0.82$ and $0.83$ (obtained, respectively, for both the methods with the help of data given in first column in Table 1).

In the current study we put emphasis on observation of the mammalian similarity through the critical muscle allometry exponent $a_{cm}^{(\exp)}$ derived in Fig.1. and on the basis of one-scale long-bone allometric data on the reduced-dimension exponent $\lambda_i^{(\exp)}$obtained in Ref. [14]. The relevant reformulation of the elastic-buckling and the elastic-bending criteria given in Eqs.(11) and (15), in terms of the observable $\lambda_i$ provides the following predictions for the critical-force exponents, namely

$$a_c^{(buckl)} = 2 < \frac{2-\lambda_i}{2+\lambda_i} b_i > \text{ and } a_c^{(bend)} =< \frac{3-\lambda_i}{2+\lambda_i} b_i > \tag{16}$$

obtained with the help of Eq.(7) and estimated in last column of Fig.1. As seen, the elastic-force bone-*buckling*-deformation mechanism, proposed by McMahon in Ref. [4] suggests estimate $a_c^{(buckl)} = 0.90$ for both the regression methods that is not justified by the data $a_{cm}^{(\exp)} = 0.81 - 0.83$. In contrast, the elastic-force bone-*bending*-deformation mechanism predicted by $a_c^{(bend)} = 0.81$ (and 0.83) within the *LSR* (and *RMA* regression) methods is proved by selfconsistent reduced-dimension and linear-dimension long-bone allometry data reported by Christiansen in Refs. [14] and Ref. [13], respectively. Again, analysis given similar to that in Table 1, for the case of the *two-scale* principal-bone data reported in Refs. [13,14], corroborates the same mechanism of evolution only for *small* mammals observed within the LSR method, but remains this question open in the case of small mammals tested by the *RMA* regression, and for all large mammals treated by both the methods.

## IV. DISCUSSION AND CONCLUSIONS

We have discussed the problem of observation of natural similarity in evolution of terrestrial mammals through the scaling laws established in skeletal allometry. Verification of the two conceivable evolution mechanisms that drive the bone size development with body mass of animals is given on the basis of experimental data on the reduced dimension ($\lambda_i = l_i/\ d_i$), longitudinal dimension ($l_i$), and transverse dimension ($d_i$) allometric exponents, commonly discussed in the mammalian long-bone allometry.

Since Galilei it was repeatedly recognized that the isometric skeletal evolution prescribed by the overall-bone exponent $\lambda_0 = 1$ is not observed in the nature because the small mammals are not geometrically overbuilt and the large species do not operate very close to their mechanical failure limit that it would be expected from the isometric scenario. This figurative, widely cited description given by Biewener [7] is in agreement with the simplified version (with $\lambda_0 = 1$) of the more sophisticated scenario proposed by McMahon. Within the ESM, the mammalian similarity was introduced [4] on the basis of realistic geometrical-shape and mechanical-force correspondence that takes place between a given skeletal bone and a rigid cylinder. As mentioned in the Introduction and illustrated in Fig.2, evolution of bone dimensions with body mass given by the ESM was disapproved in long bone allometry. This implies that the ESM prediction that $\lambda_0^{(buckl)} = 0.667$ is not so far experimentally justified by the observed data on $\lambda^{(\exp)}$, including the most systematic finding that for principal long bones $\lambda^{(\exp)} = 0.78 - 0.82$ (that follows from Table 1 as the mean between the *LSR* and *RMA* bone-averaged data).

A good deal effort has been undertaking in long bone allometry to learn experimental conditions for observation of critical-force (elastic-*buckling*-deformation and *gravity*-induced) mechanism proposed by McMahon for explanation of the anatomical adaptation of skeletal bones through their linear dimensions. The first objection [5] by Economos was that the by McMahon's mechanical-failure mechanism should not be expected as a unique for all species, but would more suitable for *large* mammals. This stimulated a careful search for additional scaling laws for small and large mammals. These were established in terms of the double sets of allometric exponents introduced [13–15] by Christiansen through the *two-scale* regressions distinguished by the boundary mass $M_c = 50kg$ adopted as common for all species. Furthermore, it was speculated that the revealed inadequate description of the scaling laws is due to inaccuracy of the methods of regression and, as a result, the *RMA* regression was suggested [13] as well-chosen instead of the traditional *LSR*. The second objection [5] by Economos refers to the *linearity* of the logarithmic scaling laws given in Eq. (2), which was not expected to be sole across the three order of magnitudes of body mass. Experimental verification of this idea by Christiansen revealed [13] that application of the polynomial type of regressions in bone allometry does not improve the correlations established within the traditional linear logarithmic scaling. Finally, thorough numerical analyses [13,14] of the reasons of the ESM failure brought Christiansen to a conclusion that "many factors contribute to maintaining skeletal stress at uniform level", including the factor of bending-deformation-induced stresses, which are more important [13] than stresses illuminated [4] by McMahon.

We have demonstrated how the factors of muscle fiber contractions, bone mass evolution, and of bending bone deformations can be incorporated into the ESM model. As a result, the *modified* (by bone-mass and muscle-contraction factors) the ESM becomes observable (see shaded area that extends $a$-buckling line in Fig.2) under condition that the unreduced statistical error of the allometric data [8,10,12] is taken into account. Otherwise, the *extended* (additionally by bending-deformation factor) ESM is experimentally justified in Fig.2. Another analysis (given in Table 1) yields the observation of the mammalian similarity within the *principal*-long-bone allometric data [13–15] by Christiansen, with systematically reduced phylogenetic statistical error. As demonstrated, this observation can be realized only in terms of the bone-*averaged* allometric exponents, restricted by the *principal* bones that are involved into the evolution-constraint equations. Example is the volume-constraint $b$-equation, which should be valid for any conceivable bone-evolution mechanism. As follows from analysis given in columns 2 and 3 in Table 1, $b$-equation is observed in the "bone-averaged" form $2d^{(\mathrm{exp})} + l^{(\mathrm{exp})} = b^{(\mathrm{exp})}$, but not in the form $2d_i^{(\mathrm{exp})} + l_i^{(\mathrm{exp})} = b_i^{(\mathrm{exp})}$ presented for a given $i$-bone. We guess that the observation of the geometric-shape similarity through experimental justification of the exact Eq.(12b) should depend on neither the number of scales nor the number of methods chosen for regression of the bone-dimension allometric data. Our additional verification of the cylindric-shape similarity given on the basis of the *two-scale* principal-long-bone allometric data (taken from Table 3 in Ref. [13]) and derived by the *LSR* and the *RMA* corroborates this statement for both small and large mammals. We infer therefore that both the methods and both the scales are equivalent in observation of the "bone-averaged" geometric mammalian similarity, at least for the principal** bones.

A crucial role of the principal bones in primarily support the body mass was highlighted by Christiansen. He noted [14] that greatly reduced *ulna* and too thin *fibula* do not play of much importance in support of body mass. They are therefore not suitable for testing of the critical-force constraints and should be excluded from the principal bone set. As follows from our analyses given in Fig.1, qualitatively the same should be referred to some muscle fiber groups such as *common digital extensors* which are not responsible for peak bone stresses. As seen from Fig. 9 in Ref. [14] and Fig.1, *tibia* and *plantaris* show a crossover behavior that corresponds to the principle-set bones and to the principle muscle-fiber groups, respectively, for small and large mammals. As the reliable *critical* principal-muscle-area exponent $a_{cm}$ $(= a_c)$, which enters the critical-force $a$-equations, we propose the data $a_{cm}^{(\mathrm{exp})} = 0.82 \pm 0.01$. This is deduced in Fig.1. and should be distinguished from the muscle-area data $a_m^{(\mathrm{exp})} = 0.80 \pm 0.03$ that was groundlessly used, instead of $a_{cm}^{(\mathrm{exp})}$, in establishing of experimental validation [20,19] of the critical-*bending*-force constraint $3d^{(\mathrm{exp})} - l^{(\mathrm{exp})} = a_{cm}^{(\mathrm{exp})}$. As shown, this equation, unlike the case of the critical-*buckling*-force constraint $4d^{(\mathrm{exp})} - 2l^{(\mathrm{exp})} = a_{cm}^{(\mathrm{exp})}$ related to the original ESM, is observable directly and indirectly through, respectively, the

**Extended statistical analysis of both the constraint equations, with including all available bone allometric data will be discussed elsewhere [24].

$a$-constraint equation and Eq.(16) (analyzed in the last column of Table 1). Again, we infer that the observation of the *bending*-force criterium does not depend on the method chosen within the one-scale regression.

This is not the case for the *two-scale* data on bone-dimension allometric exponents reported [13] by Christiansen. Indeed, as follows from our many-sided analysis, the elastic-bending criterium is definitely supported for the *small* and large mammals within the (principal-bone-averaged) *LSR* data and *RMA*, respectively. With accounting of the observation of the same criterium though the *one-scale* (principal-bone-averaged) *LSR* data, we see that correlations established by the traditional *LSR* method, unlike suggestion in Ref. [13], show their self-consistency. But no certain conclusions can be inferred within the observation windows for small and large mammals in the cases of, respectively, *RMA* regression and *LSR*. We guess that the revealed discrepancy of the two equal in rights regression methods signals on failure of definition of the observation windows employed for the analysis of the critical-force constraints. In other words, unlike the case of the cylindric-shape similarity, these windows are not expected to be universal, and cannot be therefore introduced by the unique boundary mass $M_c$.

Thereby we have demonstrated that the mammalian similarity, observable through experimental validation of the bone-evolution constraint equations, is described in terms of the *one-scale* principal-bone-*averaged* characteristics, which show independence on the regression method. Within this context, the observed in nature long-bone mammalian evolution can be described through longitudinal-to-transverse bone-dimension scaling law, with the aforegiven "method-averaged" exponent $\lambda^{(\exp)} = 0.80 \pm 0.02$. Assuming a high enough accuracy for the $i$-bone experimental data on the exponents $a_{ci}^{(\exp)}$ and $b_i^{(\exp)}$, both the discussed evolution-constraint criteria are approximated in the following forms, namely

$$\lambda^{(buckl)} = 2\frac{2b - a_{cm}}{2b + a_{cm}} \text{ and } \lambda^{(bend)} = \frac{3b - 2a_{cm}}{b + a_{cm}} \tag{17}$$

that follows from Eqs.(11) and (15), respectively. With accounting of the finding that $a_{cm}^{(\exp)} = 0.81 - 0.83$ and adopting for the bone-mass mammalian allometric exponent $b^{(\exp)} =$

1.03 − 1.06 (see column 3 in Table 1) one has the following estimates for the reduced-dimension allometric exponents:

$$\lambda^{(buckl)} = 0.87 \pm 0.02 \text{ and } \lambda^{(bend)} = 0.80 \pm 0.03 \text{ with } \lambda^{(\exp)} = 0.80 \pm 0.02 \tag{18}$$

One can see that solely the elastic-bending criterium is validated. This implies corroboration the bone evolution mechanism, which provides avoidance of mechanical failure of mammalian bones caused by critical *elastic bending* deformations induced by *maximum-area* muscle contractions in long bones achieved during peak stresses.

From the physical point of view, the fact that the bending (but not buckling) elastic deformations are crucial for mechanical failure of *long* rigid bones is expected, under condition that the inequality $L_{is} \gg D_{is}$ (but not $L_{is} \gtrapprox D_{is}$) is fulfilled for animals of arbitrary mass. This fact was not corroborated in the one-scale long-bone allometry, and we therefore report on first observation of the bending-critical-force criterium, which is expected to be universal for small and large mammals. Finally, after McMahon, we have demonstrated how the scaling laws established in mammalian allometry arise from a natural similarity of animals and how they can be quite explicit on the evolution constraints on the basis of simple geometrical and clear physical conceptions.

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| Bone | dimen sions | | reduc ed dim ensions | | | bone mass | | muscle area | |
|---|---|---|---|---|---|---|---|---|---|
| *LSR* data | $d_i$ | $l_i$ | $l_i/d_i$ | $\lambda_i$ | $b_i^*/d_i - 2$ | $2d_i + l_i$ | $b_i^*$ | buckling | bending |
| humerus | .3816 | .2996 | 0.785 | 0.763 | 0.804 | 1.063 | 1.070 | 0.927 | 0.838 |
| radius | .3868 | .2995 | 0.774 | 0.753 | 0.802 | 1.073 | 1.084 | 0.948 | 0.850 |
| femur | .3548 | .3014 | 0.849 | 0.843 | 0.988 | 1.011 | 1.060 | 0.816 | 0.714 |
| tibia | .3600 | .2571 | 0.714 | 0.764 | 0.717 | 0.977 | 0.978 | 0.926 | 0.822 |
| Averaged | .3708 | .2894 | 0.781 | 0.781 | 0.828 | 1.031 | 1.048 | 0.904 | **0.806** |
| *RMA* data | $d_i$ | $l_i$ | $l_i/d_i$ | ......$\lambda_i$ | ...$b_i/d_i{-}2$ | $2d_i + l_i$ | $b_i$ | $a_{ci}^{(buckl)}$ | $a_{ci}^{(bend)}$ |
| humerus | .3860 | .3109 | 0.805 | 0.784 | 0.806 | 1.083 | 1.083 | 0.947 | 0.862 |
| radius | .4014 | .3210 | 0.800 | 0.787 | 0.743 | 1.124 | 1.101 | 0.959 | 0.874 |
| femur | .3599 | .3089 | 0.858 | 0.864 | 0.976 | 1.029 | 1.071 | 0.850 | 0.799 |
| tibia | .3654 | .2767 | 0.757 | 0.804 | 0.731 | 1.008 | 0.998 | 0.851 | 0.781 |
| Averaged | .3782 | .3044 | 0.805 | 0.810 | 0.814 | 1.061 | 1.063 | 0.901 | **0.829** |

Table 1. Testing of the mammalian long-bone similarity through the elastic-buckling and elastic-bending criteria. Experimental data by Christiansen on the mammalian dimension allometric exponents for $i$-bone diameter $d_i$, length $l_i$, reduced dimension exponent $\lambda_i$, and bone mass $b_i$ exponents obtained by the least square regression (*LSR*) and the reduced major axis (*RMA*) regression methods are taken from Tables 2 in Refs. [13], [14] and [15], respectively. The *LSR* data for $b_i^*$ are estimated here with the help of relation $b_i^* = r_i b_i$ , where $r_i$ (correlation coefficient) and $b_i$ are corresponding data obtained by *RMA* regression. Predictions for the critical muscle-area exponents are given with the help of Eq.(16). Bone *averaged* magnitudes are found as the mean values of the corresponding mammalian allometric exponents, *e.g.*, $d = \Sigma_{i=1} d_i/4$.

REFERENCES


[1] G.B. West, J.H. Brown, and B.J. Enquist, *A general model for the origin of allometric scaling laws in biology*, Science 276 (1997) 122.

[2] G.B. West, J.H. Brown, and B.J. Enquist, *The fourth dimension of life: Fractal geometry and allometric scaling of organisms*, Science 284 (1999) 1677.

[3] O. Dreyer, *Allometric scaling and central source systems*, Phys. Rev. Lett. 87 (2001) 038101.

[4] T. A. McMahon, *Size and shape in biology*, Science 179 (1973) 1201.

[5] A. C. Economos, *Elastic and/or geometric similarity in mammalian design?*, J. Theor. Biol. 103 (1983) 167.

[6] R. M. Alexander, *Allometry of the limbs of antelopes*, J. Zool. 183 (1977) 125.

[7] A. A. Biewener, *Biomechanics of mammalian terrestrial locomotion*, Science 250 (1990) 1097.

[8] R. M. Alexander, A. S. Jayes, G. M. O. Maloiy, and E. M. Wathuta, *Allometry of the limb bones of mammals from shrews to elephant*, J. Zool. 189 (1979) 305.

[9] R. M. Alexander, A. S. Jayes, G. M. O. Maloiy, and E. M. Wathuta, *Allometry of the leg muscles of mammals*, J. Zool. 194 (1981) 539.

[10] A. A. Biewener, *Allometry of quadrupedal locomotion - the scaling of duty factor, bone curvature and limb orientation to body size*, J. Exp. Biol. 105 (1983) 147.

[11] J. E. I. Hokkanen, *Notes concerning elastic similarity*, J. Theor. Biol. 120 (1986) 499.

[12] J. E. A. Bertram and A. A. Biewener, *Allometry and curvature in the long bones of quadrupedal mammals*, J. Zool. 226 (1992) 455.

[13] P. Christiansen, *Scaling of the limb long bones to body mass in terrestrial mammals*, J.

Morphol. 239 (1999) 167.

[14] P. Christiansen, *Scaling of mammalian long bones: small and large mammals compared*, J. Zool. 247 (1999) 333.

[15] P. Christiansen, *Mass allometry of the appendicular skeleton in terrestrial mammals*, J. Morph. 251 (2002) 195.

[16] L.D. Landau and E.M. Lifshitz, *Theory of Elasticity*, Pergamon Press, London (1989).

[17] D.R. Carter, D.J. Smith, D.M. Spengler, C.H. Daly, and V.H. Frankel, *Measurement and analysis on in vivo bone strains on the canine radius and ulna,* J. Biomech. 13 (1980) 27.

[18] C.T. Rubin and L.E. Lanyon, *Dynamic strain similarity in vertebrates; an alternative to allometric limb bone scaling*, J. Theor. Biol. 107 (1984) 321.

[19] J.M.G. Garcia, M.S. Thesis, *Scaling laws in biology*, Universidade Federal de Minas Gerais, *unpublished,* (2001).

[20] D.R. Selker and D.R. Carter, *Scaling of the long bone fracture strength with animal mass,* J. Biomech. 22 (1989) 1175.

[21] A.A. Biewener, *Musculoskeletal design in relation to body size*, J. Biomech. 24 (1991) 19.

[22] C.M. Pollock and R.E. Shadwick, *Allometry of muscle, tendon, and elastic energy-storage capacity in mammals*, Am. J. Physiol. 266 (1994) R1022.

[23] R. M. Alexander, G. M. O. Maloiy, B. Hunter, and J. Nturibi, *Mechanical stresses in fast locomotionof bufalo and elefant*, J. Zool. 189 (1979) 135.

[24] J.M.G. Garcia, Silva J.K.L and V.B. Kokshenev, to be published.

# Figure Captures

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Fig. 1. Evolution of the cross-section area for muscle fibers in the mammalian hindlimbs with body mass. *Points*: diamonds, circles, squares and crosses are experimental data taken from Fig.3 in Ref. [22] for, respectively, gastrocnemius, plantaris, deep digital flexors and common digital extensors. *Solid line* corresponds to the maximum-muscle-area regression approximated from above with $A_m = 290 * M^{0.82}$. *Dashes line* - isotropic scenario description, $A_m = 29 * M^{2/3}$ . *Error bars* are due to the nearest-neighbor points found from above for the same mass.

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Fig. 2. Mammalian bone-dimension diagram: bone diameter against bone length. *Points:* **A'79**, **B'83**, **B'92** and **C'99** correspond to the overall-long-bone-averaged allometric data derived through the least square regression method by Alexander *et al.*, Biewener, Bertran & Biewener, and Christiansen and reported, respectively, in Refs. [8,10,12] and [13]. *Crosses* correspond to the ESM [4] ($d_0^{(buckl)} = 3/8$, $l_0^{(buckl)} = 1/4$, $a_0 = b_0 = 1$) and isometric scenario ($d_0 = l_0 = 1/3$, $a_0 = 2/3$, $b_0 = 1$) predictions; *a-lines* are given by the elastic-bucking and elastic-bending $a$-constraints given in, respectively, Eqs. (9) and (13) and estimated for the case of the critical-force exponent $a_c = 0.82$ derived in Fig.1. The dashed areas indicate the elastic-bucking and elastic-bending *criteria* given, respectively, in Eqs.(10) and (14). These areas extend the corresponding $a$-lines by accounting of the $b$-constraint equations within the experimental error for $a_{cm}^{(\mathrm{exp})} = 0.82 \pm 0.01$ and $b^{(\mathrm{exp})} = 1.05 \pm 0.05$ taken, respectively, from Fig. 1 and Table 1.